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DEMOGRAPHIC ASPECTS OF COEXISTENCE IN ENGELMANN SPRUCE AND SUBALPINE FIR

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ABSTRACT

The mechanisms for the maintenance of coexistence of Engelmann spruce and subalpine fir in subalpine forests of the Colorado Front Range were examined by comparing age, size, and spatial distributions of spruce and fir in two adjacent, previously logged sites of differing moisture availability. Adult tree ages were calculated from stem cores, while seedling ages were calculated from a multiple regression equation based on diameter, height, and number of branch whorls. Tree size was measured by height and diameter; spatial distributions were described by Morisita’s index of dispersion.

Cumulative age and size distributions were significantly different in the two species, with greater longevity and a larger overall size in spruce than fir. Both species showed a significant linear relationship between size and age, while fir showed a faster height growth rate than spruce. The linear relationship between age and size was much closer in seedlings than in adults. Seedling spatial distribution was highly clumped in both species, but mature trees showed little or no clumping. Because both species are mainly wind dispersed, the greater clumping in spruce than in fir seedlings suggests that spruce have more specific establishment requirements than fir. Colonization patterns indicated that spruce seedlings were primarily found in forest gaps or associated with fir canopy trees, while fir seedlings were more commonly found in the forest, associated with either spruce or fir canopy trees. Tree density, growth rates, and mortality rates were higher in the wet site, with spruce showing the largest between site differences. These data suggest a new hypothesis for coexistence stating that Engelmann spruce and subalpine fir are maintained as codominants because the greater longevity and size of spruce is balanced by the faster height growth and more flexible seedling establishment requirements of fir.

THE QUESTION of what factors permit species to coexist has long engaged both plant and animal ecologists (Hutchinson, 1959; Grubb, 1977; Werner, 1979; Brown, 1981). Accepted coexistence theory has been derived from Gause’s (1934) principle of competitive exclusion; that is, species must show niche differentiation in order to coexist. More recently, Pickett (1980) suggested that coexistence of plant species occurs either because species occupy different niches or because disturbance prevents competitive equilibrium, while Aarsen (1983) attributed coexistence of plant species to niche differentiation or reciprocal selection that maintains a balance of competitive abilities. In the present study, Engelmann spruce-subalpine fir forests were selected to examine these questions of coexistence because they are relatively simple communities in which spruce and fir coexist, often as the only two tree species present (Marr, 1961), and because they comprise a large part of the forested area in the central Rocky Mountains. According to Alexander (1974), the subalpine forests are the largest and most valuable timber resource in Colorado and Wyoming.

Although it is generally agreed that Engelmann spruce and subalpine fir coexist and form the predominant climax community in the subalpine zone of the central and northern Rocky Mountains (Daubenmire, 1943; Stahelin, 1943; Marr, 1961; Romme and Knight, 1981), the mechanisms permitting their coexistence are not clear. Four different hypotheses have been presented specifically for Engelmann spruce-subalpine fir communities: 1) Peet (1981) suggested that coexistence of spruce and fir is maintained by disturbance because, in the absence of disturbance, the greater reproductive success of fir in the understory would lead to a steady increase in the dominance of fir and the virtual elimination of spruce after about 1,000 years; 2) in Alberta, Day (1972) found that subalpine fir cannot compete with Engelmann spruce x white spruce hybrids.


(Picea engelmannii × Picea glauca) in the overstory because of early predisposition to disease and inability to withstand evaporative stress, even though fir may be four times as common as spruce in the understory (Day also suggested that in the absence of fire, spruce would decrease and fir would increase in dominance); 3) Oosting and Reed (1952) concluded that the shorter life span of subalpine fir to Engelmann spruce (300 vs. 500 yr) results in earlier death of fir canopy trees and that the prolific nature of fir maintains it as a codominant; and 4) Fox (1977) suggested that differences in seedling establishment requirements result in alternation of species in the same location and therefore coexistence. Peet's suggestion is not likely ever to be testable because, as Peet himself notes, 1,000-yr periods without disturbances are virtually unknown. Other recent studies (Harper, 1977; White, 1979; Shugart and West, 1981; Sousa, 1984) have shown that disturbance at some level is nearly universal and communities are rarely in competitive equilibrium.

The purpose of this study was to examine Hypotheses 3) and 4) by comparing the demographic characteristics of age, size, and spatial distributions in all-aged spruce-fir stands typical of those currently found in the Colorado Front Range. Most of these stands have been partially logged and the present study acknowledges this widespread situation and aims to gain a better understanding of the demography of such forest tree communities. More specifically, the role of each tree species in the community was studied by 1) comparing age and size distributions within and between populations of spruce and fir, 2) comparing patterns of spatial distribution between spruce and fir and between seedlings and adults of each species, and 3) comparing age, size, and spatial distributions of spruce and fir in two adjacent sites of differing moisture availability. It is important to examine both age and size distributions in plant populations because the plasticity and indeterminate growth form of plants often makes size a more sensitive indicator of individual interactions and microenvironmental variation than age (Johnson and Bell, 1975; Knowles and Grant, 1983). However, gaps in the age structure provide evidence of past disturbance history and successional status that may not be present in the size structure (Whipple and Dix, 1979; Lorimer, 1980). In addition, the correspondence between age and size distributions varies with different tree species (Knowles and Grant, 1983; Lorimer and Krug, 1983) and seral status (Despain, 1983). Although there are several general ecological studies that include spruce-fir forests in the central Rocky Mountains (Oosting and Reed, 1952; Marr, 1961; Peet, 1981), few workers have examined age structure (Miller, 1970; Hanley, Schmidt and Blake, 1975; Whipple and Dix, 1979; Parker and Peet, 1984) or size structure (Peet, 1981), and only Knowles and Grant (1983) have compared age and size structures. No published studies of Engelmann spruce and subalpine fir have included comparisons of age, size, and spatial distributions in seedlings and adults in different microhabitats. Both seedlings and adults are included because the probability of death for most plant species is highest in the seed and seedling stage and often declines and becomes constant during the adult period, up to senescence (Harper, 1977; Werner, 1979).

**MATERIALS AND METHODS**—The two study sites were located on Niwot Ridge, elevation 3,200 m, in the Colorado Front Range, near the University of Colorado Mountain Research Station, 10 km north of Nederland. These particular stands of Engelmann spruce, Picea engelmannii (Parry) Engelm., and subalpine fir, Abies lasiocarpa (Hook.) Nutt., were selected because: 1) their proximity (200 m) makes them replicates of each other for climatic conditions; 2) they have small, disturbed areas providing gaps for seedling establishment; and 3) they represent examples of relatively wet and dry stands found on Niwot Ridge. As with most stands in the Rocky Mountains, there is evidence of disturbance, both lumbering and fire; the area has been relatively undisturbed since 1900. The lumbering occurred 90–110 yr ago (F. Schweingruber, unpubl. data), and a count of stumps in the two sites showed that lumbering reduced the total sample size by about 20%. Only a few stems showed evidence of fire.

Plant species diversity is low in mature Engelmann spruce-subalpine fir forests. Spruce and fir are the predominant tree species, with an occasional lodgepole (Pinus contorta Dougl.) or limber pine (Pinus flexilis James) in disturbed or drier areas. The understory is covered by herbaceous species, predominately Vaccinium myrtillus L., Pedicularis racemosa Dougl., and Polemonium delictatum Rydb.

At each site, four \(2 \times 100\)-m transects were placed 10 m apart, and all individuals in 10 × 2-m plots within these transects were numbered. Division of each transect into smaller plots facilitated subsampling. Within these transects all adult trees (greater than 7.5 cm diam at breast height) and a random selection of seedlings and saplings (30–40% of those...
originally marked) were chosen so that a total of 253 spruce and 257 fir were studied. Seedlings were defined as individuals less than 0.5 m tall; saplings were individuals greater than 0.5 m tall and less than 7.5 cm diam. If two or more stems were physically connected, the group was considered to be one individual and subsequent measurements were recorded for the largest stem. Diameter and height were measured on each tree; heights greater than 2 m were measured with a clinometer. Natural log transformations of diameter and height were used successfully to normalize the data for both spruce and fir seedlings. The number of branch whors was also recorded for each seedling. Mortality estimates were made by recording the number of missing or dead individuals in each plot for the two growing seasons after they were labeled. As in most studies of long-lived tree populations, data for the present study necessarily represent one point in time.

Soil moisture was measured gravimetrically (Shea, 1985), at the 5-10-cm depth, every 2 wk during the growing season from July through September 1983. Moisture stress measurements were made directly on the trees using a pressure chamber. Measurements were taken in the field, at dawn, and at the warmest part of the day (noon to 2 p.m.) on the same days that the soil moisture samples were collected. Pressure chamber measurements were made using small branch tips, 3–5 cm long, located 1.5 m above ground, from the same three to six trees at each site for each sampling period. Sampling procedures followed those of Ritchie and Hinckley (1975) and Kaufmann and Thor (1982); equal numbers of spruce and fir trees were measured.

Tree ages—Trees larger than 2.5 cm diam were aged using tree cores taken at 30 cm above ground on the east-facing side of each tree. Ages were determined by counting rings on dried and sanded cores with a dissecting microscope. Height and age measurements on 30 spruce and 31 fir seedlings were used to calculate regression equations for predicting age at a height of 30 cm. This predicted age, 23 yr for spruce and 24 yr for fir, was added to each core measurement to estimate years lost by coring trees at 30 cm instead of ground level. If \( Y \) represents seedling age and \( X_1 \), represents height (mm), then the regression equation for spruce is \( Y = -30.03 + 9.30lnX_1 \) \( (r^2 = 0.65, P \leq 0.001) \) and for fir is \( Y = -30.48 + 9.50lnX_1 \) \( (r^2 = 0.77, P \leq 0.001) \).

Seedling ages were estimated nondestructively using multiple regression equations based on measurements of diameter, height, and number of branch whors on the same 30 spruce and 31 fir seedlings. If \( Y \) represents seedling age, \( X_1 \) represents height (mm), \( X_2 \) represents diam (mm), and \( X_3 \) represents number of branch whors, then the regression equation for spruce is \( Y = 2.07 + 2.88lnX_1 + 0.7181 \cdot lnX_2 + 0.588X_3 \) \( (r^2 = 0.82, P \leq 0.001) \) and for fir is \( Y = -12.16 + 2.36lnX_1 + 4.51 \cdot lnX_2 + 0.219X_3 \) \( (r^2 = 0.81, P \leq 0.001) \). The correlation between predicted age and actual age (for the 30 spruce and 31 fir seedlings) is \( r = 0.90 (P \leq 0.001) \). Chi-square tests showed no evidence that the age estimates for either spruce or fir were biased; that is, nearly the same number of ages were over and underestimated. Further regression analyses indicated a significant linear relationship between age and each independent variable alone, but the best age predictions were obtained by using all three variables: diameter, height, and number of branch whors. Number of branch whors in spruce and height in fir were the best single predictors of age, with correlation coefficients of \( r = 0.89 \) and \( r = 0.88 \), respectively, between predicted and actual age.

Spatial distribution.—The position of all individuals was mapped to the nearest decimeter within each transect. Maps were drawn from the \( X, Y \) coordinates by a Calcomp plotter for each species in each site. The number of individuals per quadrat was determined from these maps.

Morisita's (1959) index, \( I_b \), was chosen as a measure of clumping. The use of this measure has been described by Sakai and Oden (1983) and Goodall and West (1979). Morisita's index is given by

\[
I_b = q \sum_{i=1}^{q} n_i(n_i - 1)/N(N - 1),
\]

where \( q \) is the number of quadrats, \( n_i \) is the number of individuals of the species in the \( i \)th quadrat, and \( N \) is the total number of individuals in all \( q \) quadrats. The index \( I_b \) equals 1.0 when the population is randomly dispersed, where random implies an independent distribution of individuals in quadrats, with an equal probability of each individual occurring in any one quadrat. If the individuals are clumped, then \( I_b > 1.0 \), and if the individuals are evenly distributed or hyperdispersed, then \( I_b < 1.0 \).

Morisita's index was computed for seedlings (individuals ≤0.5 m tall) and adults (individuals >0.5 m tall) using three quadrat sizes. There were too few saplings to calculate a separate index for them. The smallest quadrat size was selected by requiring the minimum mean
of 0.6 individuals per quadrat necessary to detect clumping (Sakai and Oden, 1983). For a species in a given area the values of I, calculated for various quadrat sizes permit identification of the size at which clumping is greatest and suggest natural patch size for a given species (Morisita, 1959). The patches must be large enough to accommodate more than one individual so that clumping is a logical possibility.

RESULTS—Although tree size was measured by both diameter and height, the two variables had similar patterns, and in this discussion diameter will represent size unless otherwise specified. The Pearson product-moment correlation between height and diameter, based on all individuals studied, was highly significant in both species ($P \leq 0.001$), $r = 0.97$ for spruce and $r = 0.95$ for fir. For clarity in presentation, measurements were grouped using 10-yr age classes, 1-cm diam classes, and 0.5-m height classes.

The age and size frequency distributions (Fig. 1, 2) showed similar trends within each species and similar patterns between spruce and fir. The largest percentage of individuals was in the smallest size class in both species. Over 40% of the spruces and over 50% of the firs were in the 1-cm diam or smaller size class. In both spruce and fir the age class distribution showed a lower peak than the size class distribution, with nearly 30% of the spruce and nearly 50% of the fir individuals in the 20 yr or younger age classes. Both species also had a small peak in the age class distribution around 100 yr, with nearly 15% of the individuals in the 90–110 yr age classes. This peak was not evident in the size class distribution. While the range of age and size distributions was similar in the two species, fir had a larger proportion of smaller and younger individuals than spruce.

Cumulative age and size distribution curves (Fig. 3, 4) further facilitate comparison between species. The curves represent net survivorship, which is composed of each class's establishment minus mortality of all previous classes. As tested by the Kolmogorov-Smirnov goodness-of-fit procedure, spruce and fir had significantly different age class and size class distributions. Spruce had a higher proportion of older individuals than fir in each age class, and both species had a steady decline in proportion of individuals with increasing age. The fir age distribution leveled off at 250 yr, while the spruce distribution showed a fairly steady decline through all age classes. Size distribution showed the same general pattern, with spruce having a higher proportion of larger individuals in each size class than fir. When trees in the postlogging population, that is, trees less than 110 yr old, were compared, age and size distributions were still significantly different between species ($P \leq 0.01$ for age and size), with spruce having a higher proportion of older or larger individuals in each class.

Regression analyses were used to examine the relationship between size and age (Fig. 5). In both species, diameter and height showed a significant linear relationship with age ($P \leq 0.001$). An a posteriori test showed that the regression coefficients for height, but not diameter, were significantly different ($P \leq 0.01$) in spruce and fir. The larger regression coefficient for height in fir suggested that fir may grow in height at a faster rate than spruce. The proportion of variation explained by these equations ($r^2$, the coefficient of determination) varied from 0.61 to 0.72. When only trees ≥2 m tall were included in the analyses, there was
still a significant linear relationship of diam and height on age ($P \leq 0.001$). However, the $r^2$ for diam vs. age decreased to 0.18 ($b = 0.06$) in fir and 0.43 ($b = 0.07$) in spruce; $r^2$ for height vs. age was 0.08 ($b = 0.02$) in fir and 0.38 ($b = 0.03$) in spruce.

**Microenvironmental variation**—Examination of between-site variation showed that population demographic characteristics can vary over short distances ($\leq 200$ m). Moisture availability was the most noticeable environmental difference between the two sites as evident in both the soil and tree measurements. For 1970–1982 the mean total precipitation for the 9-mo period, January through September, at the C-1 site on Niwot Ridge (elevation 3,000 m) was 552 mm, as compared to 692 mm for January through September 1983 (Losleben, 1983). Although precipitation was above normal in 1983, percent soil moisture and maximum plant water potential measurements averaged over the 1983 growing season were significantly different between the two sites (soil moisture averaged 113.3 ± 9.0% wet site vs. 86.5 ± 8.4% dry site, $P \leq 0.05$; Pmax averaged $-1.27 \pm 0.04$ MPa wet site vs. $-1.46 \pm 0.04$ MPa dry site, $P \leq 0.001$; Pmin averaged $-0.68 \pm 0.03$ wet site vs. $-0.65 \pm 0.03$ dry site, not significantly different). Pmin and Pmax refer to the mean predawn and midday xylem pressure potential measurements. Because there were no significant differences in moisture stress between species, Pmin and Pmax values for spruce and fir were combined to examine between-site differences. The fact that Pmin (minimum xylem pressure potential) was not significantly different between the sites suggests that differences in plant water stress occurred during the hottest part of the day, but not at night. In addition, the Pmin and Pmax values of −0.6 to −1.5 MPa indicated that the trees were not under severe water stress, assumed to begin at xylem pressure potential measurements higher than −2.0 MPa (Ritchie and Hinckley, 1975). Soil moisture decreased significantly over the growing season; however, Pmax values varied depending on rain and cloud cover.

Total tree density, which includes both spruce and fir (Table 1), was significantly higher (1.26 stems/m²) in the wet site than in the dry site (0.68 stems/m²). Part of the high density in the wet site resulted from high-density seedling patches, but basal area was also greater in the wet site. Mature trees in the wet site occupied
TABLE 1. Mean and 95% confidence intervals (in parentheses) for sizes and ages of adult and seedling spruce and fir at two sites. Adults are trees ≥2 m tall and ≥7.5 cm diam; seedlings are ≤0.5 m tall. * Denotes significant differences between sites, **P ≤ 0.05, ***P ≤ 0.01, ****P ≤ 0.001

<table>
<thead>
<tr>
<th>Measurement</th>
<th>Wet site (1.26 stems/m²)</th>
<th>Dry site (0.68 stems/m²)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>N = 27</td>
<td>N = 54</td>
</tr>
<tr>
<td>Engelmann spruce</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Diameter (cm)</td>
<td>20.71 (16.48-24.94)</td>
<td>19.44 (17.65-21.22)</td>
</tr>
<tr>
<td>Height (m)</td>
<td>10.64 (9.06-12.23)</td>
<td>9.74 (8.96-10.51)</td>
</tr>
<tr>
<td>Age (yr)***</td>
<td>144 (116-173)</td>
<td>233 (213-254)</td>
</tr>
<tr>
<td>Subalpine fir</td>
<td>N = 29</td>
<td>N = 37</td>
</tr>
<tr>
<td>Diameter (cm)**</td>
<td>19.93 (16.51-23.35)</td>
<td>14.49 (12.44-16.55)</td>
</tr>
<tr>
<td>Height (m)**</td>
<td>10.99 (9.66-12.31)</td>
<td>7.92 (6.93-8.91)</td>
</tr>
<tr>
<td>Age (yr)**</td>
<td>130 (104-157)</td>
<td>161 (143-179)</td>
</tr>
<tr>
<td>B. Seedlings</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Engelmann spruce</td>
<td>N = 69</td>
<td>N = 40</td>
</tr>
<tr>
<td>Diameter (cm)</td>
<td>0.42 (0.38-0.48)</td>
<td>0.50 (0.42-0.59)</td>
</tr>
<tr>
<td>Height (m)</td>
<td>0.19 (0.17-0.21)</td>
<td>0.17 (0.14-0.20)</td>
</tr>
<tr>
<td>Age (yr)</td>
<td>17 (16-18)</td>
<td>17 (15-18)</td>
</tr>
<tr>
<td>No. branch whorls</td>
<td>13 (11-14)</td>
<td>11 (9-13)</td>
</tr>
<tr>
<td>Subalpine fir</td>
<td>N = 75</td>
<td>N = 68</td>
</tr>
<tr>
<td>Diameter (cm)</td>
<td>0.34 (0.30-0.40)</td>
<td>0.33 (0.28-0.39)</td>
</tr>
<tr>
<td>Height (m)</td>
<td>0.11 (0.10-0.13)</td>
<td>0.12 (0.10-0.13)</td>
</tr>
<tr>
<td>Age (yr)</td>
<td>14 (13-15)</td>
<td>14 (12-15)</td>
</tr>
<tr>
<td>No. branch whorls</td>
<td>8 (6-9)</td>
<td>7 (6-9)</td>
</tr>
</tbody>
</table>

55.6 m² per hectare, as compared to 31.2 m² per hectare in the dry site. There were also differences in basal area occupied by each species in each site. Mature spruce trees occupied 51.3% (48.7% for fir) of the basal area in the wet site, as compared to 71.2% (28.8% for fir) of the basal area in the dry site.

Mean sizes and ages in the two sites showed different patterns for adult spruce and fir (Table 1). Both species had a significantly higher mean age in the dry site than in the wet site (P ≤ 0.001 for spruce, P ≤ 0.05 for fir). Spruce showed no significant size differences between sites, while fir trees were significantly larger (P ≤ 0.01) in diam and height in the wet site. Because trees in the wet site were the same size or larger than trees in the dry site, both species had faster growth rates in the wet site. Because of the large age differences between sites, heights and diameters were also compared using age as a covariate. With age as the covariate, adult spruce diams (24.52-cm wet site vs. 17.38-cm dry site) were significantly different between sites (P ≤ 0.001), but heights (12.32 m wet site vs. 9.2 m dry site) were not. In a similar analysis for fir, diams (20.81-cm wet site vs. 13.81-cm dry site) and heights (11.10-m wet site vs. 7.73-m dry site) were significantly different between sites (P ≤ 0.001 for diam, P ≤ 0.05 for height).

The seedlings showed a pattern of size variation different from the adults (Table 1). For both spruce and fir seedlings, univariate analysis of variance tests for each character measured showed no significant differences between the wet and dry sites. Since the size

<table>
<thead>
<tr>
<th>Quadrat size (m²)</th>
<th>No. of quadrats</th>
<th>Spruce Adults</th>
<th>Fir Seeds</th>
<th>Adults</th>
</tr>
</thead>
<tbody>
<tr>
<td>A. Wet site</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>4</td>
<td>96</td>
<td>(N = 69) 9.33*</td>
<td>0.81</td>
<td>3.18*</td>
</tr>
<tr>
<td>16</td>
<td>24</td>
<td>4.24*</td>
<td>0.98</td>
<td>1.88*</td>
</tr>
<tr>
<td>64</td>
<td>6</td>
<td>1.87*</td>
<td>0.95</td>
<td>1.30</td>
</tr>
<tr>
<td>B. Dry site</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>8</td>
<td>96</td>
<td>(N = 40) 6.65*</td>
<td>1.44</td>
<td>1.85*</td>
</tr>
<tr>
<td>16</td>
<td>48</td>
<td>4.12*</td>
<td>1.13</td>
<td>1.64*</td>
</tr>
<tr>
<td>64</td>
<td>12</td>
<td>1.71*</td>
<td>1.10</td>
<td>1.16*</td>
</tr>
</tbody>
</table>
measures were intercorrelated, multivariate analysis of variance (manova) was used to determine if the combined effects of diameter, height, and number of branch whorls produced differences between sites. Spruce seedlings were significantly different (Wilks's lambda = 0.788, $P \leq 0.001$) between sites, but fir seedlings were not. A discriminant function analysis correctly classified 76% of the spruce seedlings as coming from the wet or dry site, and diameter was twice as important as either branch whorls or height in determining group membership.

Spatial distribution, which is influenced largely by competition and microhabitat variation, may be described by three general patterns: 1) uniform, 2) random, and 3) clumped (Hutchinson, 1953). Uniform patterns indicate competition; clumped patterns suggest mutualisms or microenvironmental variation. A random pattern may result from the absence of interactive forces between individuals in a population or from disturbance factors, such as climate or predation (Gill, 1975). In both sites, spruce and fir seedlings were significantly clumped, while the adult trees showed a nearly random distribution (Table 2). Spruce seedlings were consistently more clumped than fir seedlings, and seedlings of both species were more clumped in the wet than in the dry site. The patterns were reversed for adult trees; fir adults showed a higher degree of clumping than spruce adults, and adults of both species were more clumped in the dry than in the wet site. The adult dry site fir were significantly clumped, showing as much clumping as the seedlings at the smaller quadrat sizes.

A comparison of presence or absence of seedlings in 10 × 2-m plots throughout the sites showed that at least one spruce or fir seedling was present in most plots in the wet site (Table 3). Fir seedlings in the dry site were more than three times as common as spruce seedlings and were present in 90% of the plots, while spruce seedlings were present in only half the plots. In addition, seedling density and mortality for both species were greater in the wet than in the dry site.

Examination of the locations of spruce and fir seedlings (Table 4) showed that spruce were more common in the forest gaps and fir were more common in the forest. Dry site gaps had a smaller proportion of the total seedlings, with almost no fir seedlings. In both sites, spruce seedlings were more commonly found in plots with dominant fir rather than dominant spruce trees. Fir seedlings were more common under dominant fir trees in the wet site and equally common under dominant fir and dominant spruce trees in the dry site.

**DISCUSSION**—The overall patterns of the age and size distributions examined here support Oosting and Reed's (1952) findings that spruce has greater longevity and a larger average size than fir, and they also indicate a steady rate of replacement, as opposed to major bursts of successful establishment, in both species over several centuries. Although instantaneous age data are not adequate for determination of the exact proportions of recruitment and mortality, I suggest that the age distributions in this study were predominately shaped by mortality of seeds and seedlings. While the large numbers of seeds produced (Alexander and Engelby, 1983; Shea, unpubl. data) enable these species to respond to large disturbances with increased seedling survival, the data showing a relatively constant number of survivors per age class suggest that mortality is largely density dependent. That is, as more seeds are shed, mortality rates increase at the seed and early seedling stages, resulting in approximately the same number
of individuals in each age class (Hett, 1971; Harper, 1977). In this study no single 10-yr age class over 30 yr had more than 10% of the individuals sampled. I also examined the data in 1-yr age classes to determine if grouping trees into age and size classes may have partially obscured peaks of establishment. The number of individuals in 1-yr age classes (ungrouped data) showed that cohorts over 30 yr of age usually had one to three individuals. The largest cohorts were 12- and 13-yr-olds in fir, each with 13 individuals (5%), and 14-yr-olds in spruce, with 10 individuals (4%). Over the age span of the trees studied, no individuals represented 62% of the years for spruce and 68% of the years for fir. Similar data were obtained by Knowles and Grant (1983), who also concluded that mortality dominates the shape of the age and size distributions in the conifer species they studied, which included Engelmann spruce. Parker and Peet (1984) believe that cumulative age curves are shaped at least as much by establishment as mortality in stands recovering from disturbance.

Although the cumulative age and size class distributions of spruce and fir differed statistically between species, they were similar in shape. Their shape suggests that the stands were all-aged and had experienced decreasing mortality with age. The negative power function model, a mathematical description of decreasing rate of mortality with age, describes the age structure distribution of most shade tolerant tree species (Hett and Loucks, 1976). Whipple and Dix (1979) found similarly shaped, inverse-J, age distributions in spruce and fir stands in Colorado, although they also found bimodal and decreasing patterns. A bimodal age distribution for Engelmann spruce (Miller, 1970) in western Colorado was attributed to epidemics of Engelmann spruce beetle, while in the same population subalpine fir had an inverse-J age distribution. Peet (1981) found bell-shaped diameter distributions in younger, even-aged stands, and inverse-J diameter distributions in all-size stands of spruce and fir in Colorado.

The information provided by age and size distributions is often similar (Lorimer, 1980), a conclusion supported by the overall similarity of the age and size distributions in this study, but some information on stand history may be lost by examining size distributions alone. For example, the small peaks in the frequency age distributions of both spruce and fir at 90–110 yr were absent in the size distributions. These peaks are likely the result of seedling establishment after disturbance, such as the lumbering, in the late 1800’s (Knowles, 1980; F. Schweingruber, unpubl. data). In addition, the similarity of the age and size distributions may be influenced by the age and size range of individuals sampled. Knowles and Grant (1983) found larger differences between age and size frequency distributions in the conifer species they studied, as did Linhart et al. (1981) for ponderosa pine (Pinus ponderosa). However, these results are not directly comparable to my study because Knowles and Grant did not include seedlings, and in the Linhart et al. study fewer than 10% of the individuals were seedlings. The linear regression analyses of size on age presented here showed a close relationship between the two variables, with age explaining 60–70% of the variation observed in size. The lower coefficients of determination ($r^2$, see Results section) for mature trees alone are closer to values found by Knowles and Grant and indicate that the relationship between age and size is closer in seedlings than in adult trees. Also, it is important to note that outliers (in this case the large number of seedlings) have a greater statistical effect (leverage) in correlation and regression than numbers in the middle of the distribution.

**Microenvironmental variation**—Between-site comparisons showed that species-specific differences persisted despite microenvironmental variation, but that site differences affected the relative frequencies of spruce and fir, as well as the magnitude of the differences in other demographic characteristics. Only the dry site data (Tables 3 and 4) support the conclusions of Oosting and Reed (1952), Day (1972), and Peet (1981) that fir seedlings are more common than spruce seedlings. However, the higher frequency of spruce and lower frequency of fir seedlings in the wet site were largely the result of a few highly clumped seedling patches in forest gaps with adequate light and moisture.

Between-site differences in age, size, and mortality show a faster growth rate and suggest a higher mortality rate for trees in the wet site. Because moisture was the only prominent environmental difference between the sites, I conclude that moisture was an important factor contributing to the increased growth and mortality rates. Growth rate differences between sites were not as readily apparent in the seedlings, which suggests that it took many years of slightly lower growth rates in the dry site for the size differences to become measurable. Diameter was more sensitive to microenvironmental variation than height for mature trees of these species. Reasons for the adult age differences between sites may be found in dis-
turbance and/or mortality patterns. The presence of more stumps in the wet than in the dry site suggests more logging damage in the wet site. The presence of recently downed mature trees only in the wet site suggests a higher rate of mortality for wet site mature trees, as well as seedlings (Table 3). Moisture in the wet site may make the mature trees more susceptible to disease and decrease stability of root systems. The more common causes of mortality in mature spruce and fir are windfall, insects, and disease (Alexander, Shearer and Shepperd, 1984; Alexander and Shepperd, 1984). For seedlings, the extra moisture may result in more germination, higher seedling density, and, consequently, higher seedling mortality.

Because spruce and fir are mainly wind dispersed, the greater clumping in spruce than in fir seedlings suggests that spruce seedlings have more specific establishment requirements than fir. These results support the findings of Noble and Ronco (1978) that spruce is more exacting in its seedbed requirements than fir and that seedbeds with exposed mineral soil are most favorable for spruce. A few squirrel caches were found that contained both spruce and fir seeds, but their location and infrequent occurrence suggest that they are a minor source of seedling establishment. Because clumping in seedlings was greatest at the smallest quadrat sizes, natural patches are probably fairly small or less than 20 m². The higher degree of seedling clumping in the wet site is likely the result of more favorable patches, in terms of light, moisture, and soil in the wet site. The lack of significant clumping in adults, except for the smaller quadrat sizes in fir in the dry site, suggests that most of the area studied was favorable for tree growth and that competitive interactions, density dependent mortality, and/or disturbance decrease clumping as trees mature. Veblen, Schlegel and Escobar R. (1980) found that favorable patches were largely responsible for significantly greater clumping (measured by Morisita’s index) in seedlings than in adults in Nothofagus forests in Chile, while in Costa Rica, Hubbell (1979) found various clumping patterns in seedlings and adults, depending on species, seed dispersal, predation, competition, and microenvironment.

The colonization patterns observed only partially support Fox’s (1977) hypothesis, in that my data indicate different establishment requirements for spruce and fir, but not that spruce and fir replace one another because seedlings of one species are associated with canopy trees of the opposite species. The location of spruce seedlings suggests that they will succeed fir canopy trees or become established in small open areas. The location of fir seedlings suggests that they have a wider range of tolerances that enables them to become established under both spruce and fir canopy trees, and in some cases, in forest gaps as well. Because there was at least one seedling of each species in most plots (Table 3), the high degree of clumping was not the result of distribution mechanisms, but rather results from the distribution of favorable habitat patches.

My height regressions, which show faster growth in fir than spruce, are supported by studies on saplings by McCaughey and Schmidt (1982) and newly germinated seedlings by Knapp and Smith (1982). Although other studies have found faster growth rates in spruce (Schmid and Hinds, 1974; Peet, 1981), different habitat conditions and the age range of individuals sampled may determine which species grows faster. Spruce seedlings in this study were generally larger than fir seedlings because of their greater average age and propensity to colonize areas with greater light availability. Colonization patterns may also explain the size differences between sites found in spruce, but not fir seedlings. Fir establishment locations were similar in the two sites, while the extra moisture in the wet site gaps led to higher density seedling patches, with taller and thinner spruce plants.

Because only two sites were examined in this study, the between-site differences observed in seedling frequency, seedling establishment patterns, and adult sizes and ages need further study. Other possible explanations (besides moisture) for the observed site differences are sampling error or disturbance. While disturbances such as logging, fire, disease, herbivory, etc. undoubtedly had a cumulative effect on the site age differences, the patterns of differences in seedling frequency, seedling establishment, and adult sizes are more parsimoniously explained in terms of the significant environmental differences between the sites. Although I suggest moisture as the likely environmental factor affecting size and establishment patterns in these species, the point is that microenvironmental variation can cause significant differences in demographic characteristics and, in turn, community structure.

In answer to the question of how spruce and fir coexist, the published hypotheses were only partially supported. The results of this study suggest a new hypothesis stating that coexistence is maintained by the greater longevity and size of spruce, balanced by the faster height growth rate and less-specific seedling establishment requirements of fir. While spruce and fir no doubt compete for resources, their dif-
ferent demographic characteristics allow each to be at a selective advantage in different microhabitats. The niche differentiation observed between spruce and fir seems to result in a balance of competitive abilities, as described by Aarssen (1983). Maintenance of this balance depends on small disturbances, such as individual tree falls, to provide canopy openings where spruce seedlings have the selective advantage. Although fir seedlings tend to be more shade tolerant and more numerous than spruce seedlings in the forest, the higher mortality rate, shorter life span, and smaller size of fir provide enough canopy openings to prevent the dominance of fir over spruce. As found by Forcier (1975) in beech, sugar maple, and yellow birch forests in New Hampshire and by Hett and Loucks (1976) in hemlock and balsam fir forests of Ontario and Wisconsin, my results indicate that the different life history characteristics of spruce and fir allow them to coexist and form what is generally considered a stable or climax community.

LITERATURE CITED


MILLER, P. C. 1970. Age distributions of spruce and fir


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